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Impacts of a Natural Disturbance on Coral Reefs in the Florida Keys and Subsequent Recovery Potential of the Sea Urchin *Diadema antillarum*

Julia Nicole Kobelt
Montclair State University

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ABSTRACT

Ecosystem resilience is a measure of an ecosystem's capacity to resist abrupt change and recover following a disturbance. While stochastic disturbances can contribute to normal ecosystem functioning, mounting natural and anthropogenic stressors are simultaneously intensifying the severity of disturbances and reducing the capacity for ecosystem recovery. Here, I examine the impacts of hurricane disturbance on a coral reef ecosystem and the potential for post-storm population recovery of a keystone herbivore, the sea urchin *Diadema antillarum*. Grazing pressure exerted by dense populations of *D. antillarum* is critical to coral reef ecosystem health by preventing (or reversing) an ecological regime shift from coral- to macroalgal-dominated reefs following disturbance. Hurricane Irma, a Category 4 Hurricane, made landfall in the Florida Keys in September 2017. The effects of the storm on *D. antillarum* and the surrounding coral reef community were evaluated at 10 sites in the middle and upper Florida Keys. Following Hurricane Irma, *D. antillarum* densities declined by 80% and the coral reef community was significantly altered. To assess the potential for local *D. antillarum* recovery, larval influx and subsequent increases in adults were measured using artificial settlement plates and transect surveys, respectively. Larval influx did not yield a measurable increase in adults over the period of the study, indicating limits to post-storm population recovery. The reestablishment of *D. antillarum* populations seems unlikely without extensive management efforts. Enhancing herbivory on coral reefs will be essential to building ecosystem resilience in the face of an increasingly severe disturbance regime.

MONTCLAIR STATE UNIVERSITY

**Impacts of a natural disturbance on coral reefs in the Florida Keys and subsequent
recovery potential of the sea urchin *Diadema antillarum***

by

Julia N. Kobelt

A Master's Thesis Submitted to the Faculty of

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Thesis Committee:

[REDACTED]

Dr. Colette Feehan

[REDACTED]

Dr. Paul Bologna

[REDACTED]

Dr. Meiyin Wu

IMPACTS OF A NATURAL DISTURBANCE ON CORAL REEFS IN THE
FLORIDA KEYS AND SUBSEQUENT RECOVERY POTENTIAL
OF THE SEA URCHIN *DIADEMA ANTILLARUM*

A THESIS

Submitted in partial fulfillment of the
requirements For the degree of Master of Science

by

JULIA N. KOBELT

Montclair State University

Montclair, NJ

2019

MONTCLAIR STATE UNIVERSITY

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CHAPTER 1

INTRODUCTION

Abrupt and persistent changes in ecosystem structure and function, or ‘regime shifts’, are becoming increasingly common in ocean ecosystems due to intensifying anthropogenic stressors that diminish ecosystem resiliency, such as overharvesting, climate change, and pollution (Nyström et al. 2000; Folke et al. 2004). Ecological resiliency measures the ability of a system to regain ecosystem structure and function following disturbance (Holling 1973). The resiliency of many coastal ecosystems, including kelp forests (Estes 1974), seagrass beds (Gunderson 2001), and coral reefs (Hughes et al. 1994) has been linked to the intensity of herbivory, with regime shifts occurring following changes in the abundance of herbivore populations (Bellwood et al. 2004). These coastal ecosystems can exhibit multiple stable equilibria, or alternative stable states, maintained by a suite of feedback mechanisms that make regime shifts difficult to reverse (Scheffer et al. 2001; Beisner et al. 2003).

On Caribbean coral reefs, intense grazing pressure by diverse assemblages of herbivorous fishes and invertebrates regulates algal abundance and stabilizes a coral-dominated ecosystem state by indirectly facilitating coral settlement (Edmunds and Carpenter 2001; Hughes et al. 2007; Mumby et al. 2007b), growth (Lirman 2001; Idjadi et al. 2010), and survival (Hughes et al. 2007). Following historical overharvesting of herbivorous fishes, the long-spined sea urchin *Diadema antillarum* became one of the last abundant grazers on Caribbean reefs (Hughes et al. 1994). This loss of functional redundancy decreased ecosystem resiliency and precipitated a regime shift to algal dominance following a disease-induced mass mortality of *D. antillarum* in 1983–84 (Hughes et al. 1994; Nyström et al. 2000). Regime shifts on Caribbean reefs from a coral-dominated to an algal-dominated ecosystem state also have been attributed to declines in coral health and abundance caused by bleaching, disease, and hurricanes (Hughes et al. 1994; Knowlton 1992; Jackson et al. 2014).

The 1983–84 mass mortality event reduced *D. antillarum* population abundance by two orders of magnitude (93 to 100% decline) throughout the Caribbean (Lessios 1988). Most *D. antillarum* populations have shown very limited recovery and have not returned to pre-mass mortality levels (Lessios 2016). The feeding preferences and grazing behavior of *D. antillarum* makes the species particularly effective at maintaining the coral-dominated state (Adam et al. 2015). Accordingly, on reefs where *D. antillarum* populations are recovering, algal cover has decreased while coral recruitment, growth, and survival have increased, and a reversal to a coral-dominated community has been initiated (Edmunds and Carpenter 2001; Myhre and Acevedo-Gutierrez 2007; Furman and Heck 2009; Idjadi et al. 2010). *D. antillarum* has yet to recover in the Florida Keys, potentially due to 1) recurrent disease outbreaks (Forcucci 1994), 2) high mortality at early life-history stages (Miller et al. 2009), 3) a lack of suitable refuge habitat from predators (Chiappone et al. 2013), and 4) low reproductive success (Feehan et al. 2016). Physical disturbances such as strong storms also may play a role (Chiappone et al. 2013; Lessios 2016), however this has not been investigated in the Florida Keys. In this thesis, I examine the effects of a hurricane disturbance event on *D. antillarum* in the Florida Keys and the potential for the population to recover following disturbance.

CHAPTER 2

LOCALIZED IMPACTS OF HURRICANE IRMA ON *DIADEMA ANTILLARUM* AND CORAL REEF COMMUNITY STRUCTURE

2.1 ABSTRACT

Strong physical disturbance from hurricanes can disrupt coral reef ecosystems and precipitate a regime shift toward algal dominance, particularly in the absence of grazing pressure to regulate algal growth post-storm. Here, I examine the influence of Hurricane Irma on a keystone grazer, *Diadema antillarum*, and the surrounding coral reef benthic community in the Florida Keys. *D. antillarum* densities and test diameters, as well as percent cover of coral reef benthic groups, were measured at 10 sites in the middle and upper Keys before and after Irma. Significant decreases in mean *D. antillarum* density and median test diameter were observed following the storm. There was a correlation between the magnitude of decline in *D. antillarum* density and the magnitude of sediment deposition on reefs, suggesting that abrasion or burial from sediment transport may have contributed to *D. antillarum* mortality. I detected significant decreases in the percent cover of sponges and hydrocorals following the storm, but no change in scleractinian coral cover, which was very low (3% mean cover) at the onset of the study. Macroalgal cover increased at sites in the upper Keys and decreased at sites in the middle Keys. There was no relationship between post-storm *D. antillarum* density and the change in percent cover of macroalgae or TAS, likely due to low overall abundance of the grazer. I predict that coral reefs will remain in an algal-dominated ecosystem state due to, among other factors, increasing frequency of strong hurricanes that impact the *D. antillarum* population.

2.2 INTRODUCTION

Hurricanes are acute perturbations that can temporarily disrupt coral reef community structure through dislodgement, abrasion, and burial of benthic organisms from intense wave energy, resulting in mortality (Woodley et al. 1981). Although hurricanes are part of a natural disturbance regime on coral reefs, human activities have changed the capacity of the reef ecosystem to recover from hurricane disturbance (Connell 1978; Nyström et al. 2000). The disturbance regime itself is also being altered, since the frequency of high-intensity hurricanes is predicted to increase due to anthropogenic climate change (Knutson et al. 2010; Cheal et al. 2017). Post-hurricane recovery to a coral-dominated state can be facilitated by herbivorous grazers regulating algal growth in newly opened spaces, but herbivore abundance may also be impacted by hurricane disturbance through direct (e.g. mortality) or indirect (e.g. reduced refuge habitat) storm effects (Bellwood et al. 2004; Mumby et al. 2006).

In the Caribbean, the impact of hurricanes on *D. antillarum* can be unpredictable. Local *D. antillarum* population density has been documented to decrease (Woodley et al. 1981) or remain stable (Aronson 1993; Jorgenson et al. 2008) following hurricane disturbance, and the factors driving these varied responses are not clear. Prior to the Caribbean-wide *D. antillarum* mass mortality event in 1983–84, Hurricane Allen in 1980 reduced *D. antillarum* density from 7.98 urchin m⁻² to 3.85 urchin m⁻² on shallow (5 to 8

m) but not deep (10 to 20 m) Jamaican fore reefs (a more wave-exposed habitat relative to the back reef) within 2 months post-storm (Woodley et al. 1981). In contrast, persistence of *D. antillarum* on shallow (1 to 3 m) back reefs was documented 2.5 months after Hurricane Dean in Southern Mexico (7.29 urchin m⁻² pre-storm and 12.6 urchin m⁻² post-storm) (Jorgensen et al. 2008). *D. antillarum* densities on shallow (1 to 2 m) back reefs were also unchanged following Hurricane Gilbert (1988, Jamaica) and Hurricane Hugo (1989, U.S. Virgin Islands) (Aronson 1993). Since Hurricanes Allen, Dean, and Hugo were all extremely powerful (Category 4 to 5) hurricanes with similar potential to impact coral reef communities, discrepancies in storm impacts on *D. antillarum* may be attributed to local reef characteristics (e.g. depth and wave exposure). Additionally, physical structures on reefs dissipate wave energy and can minimize hurricane disturbance (Steiner 2003); thus, reef three-dimensional structure may be important in determining localized impacts on marine organisms. Studies at local scales will therefore be important for understanding hurricane impacts on *D. antillarum* in order to predict and manage Caribbean coral reefs given the importance of this grazer in mediating coral-algal regime shifts.

Here, I examine the initial (within 2.5 months) impacts on *D. antillarum* and the surrounding reef community of Hurricane Irma, a powerful Category 4 storm that made landfall in the lower Florida Keys on 10 September 2017 (Cangialosi et al. 2018). I test the hypothesis that disturbance from Hurricane Irma has the potential to reduce the already low-density *D. antillarum* population on degraded coral reefs in the Florida Keys. These reefs have exceptionally low three-dimensional structure due to low coral cover (Schutte et al. 2010). I expected that large *D. antillarum* would suffer from a lack of coral habitat more so than small *D. antillarum*, which are able to hide in smaller reef crevices (Randall et al. 1964), and I therefore predicted that the size structure of the population would shift toward smaller individuals following the storm. Hurricane impacts on benthic communities can vary with proximity to the storm (Woodley et al. 1981), and I expected that reefs closer to the eye of Irma (middle Keys) would be more damaged than reefs farther from Irma's path (upper Keys). Since sediment abrasion is a potential source of hurricane-induced mortality for benthic organisms such as corals and sponges (Woodley et al. 1981), I predicted that *D. antillarum* decline would be greatest at locations with higher magnitudes of sediment transport. I also predicted that greater algal colonization would occur in locations of lower post-storm *D. antillarum* abundance, given the role of *D. antillarum* as a keystone grazer. To test these predictions, I examined *D. antillarum* density and size structure, and coral reef community structure before and after the storm at 10 sites spanning the middle and upper Florida Keys.

2.3 METHODS

2.3.1 Study Sites and Experimental Design

The impacts of Hurricane Irma on *D. antillarum* and the surrounding benthic community were assessed at a total of 10 inshore patch reef, rubble reef flat, and offshore bank-barrier reef sites, spanning 3 to 6 m maximum depth and 80 km (linear distance) of the middle (n = 7 sites: DS, EFM, EW, TP, TR, WS, WT) and the upper (n = 3 sites: PP, PR, PS) Florida Keys (Table 2.1; Fig. 2.1). Sites were sampled 1 to 3 months prior to Hurricane Irma (10 to 15 June and 2 to 3 August 2017) as part of a separate study examining

recovery of *D. antillarum* following historical disease-induced mass mortality events (C.J. Feehan unpublished data). To assess storm impacts, all sites were resampled by divers at the Florida Wildlife Research Institute (FWRI) 2.5 months (21 to 29 November 2017) after the storm, aside from a single location in the middle Keys (WT) that was sampled 4 months after the storm (9 to 11 January 2017) due to poor visibility in November (Fig. 2.1). I employed a stratified random sampling design with 2 belt transects (60×2 m) placed in the east-west direction ~ 10 m apart at each site. Permanent transects were not fixed to the substratum for repeat sampling, but site landmarks were used to place the transects in the same general location on the reef during each sampling period. Fewer sites were sampled in the upper Keys than in the middle Keys due to logistical constraints of transporting divers and gear to the upper Keys from the Florida Wildlife Research Institute in the middle Keys.

2.3.2 Physical Oceanographic Effects of the Storm

I examined time series of bottom ocean temperatures at 3 sites spanning the study region (EW, TR, and PP; Fig. 2.1) as an indicator of ocean mixing caused by the passage of Hurricane Irma. Based on the storm track, I expected greater physical impacts in the middle versus upper Keys. Temperature data were collected at hourly intervals with HOBO Pendant[®] Temperature/Light 8K data loggers (Onset Computer) attached to concrete blocks on sand bottom adjacent to the reef at each site. Mean daily temperatures were plotted over a 6-week period from 1 September to 13 October 2017 encompassing landfall of the hurricane.

To examine Hurricane Irma's impact on ocean wave heights, significant wave heights (mean height of highest one third of waves) in the study region were examined. Data were received from a physical oceanographer at Rutgers University (Travis Miles). Data were extracted from the National Oceanographic and Atmospheric Administration (NOAA) wave model hindcasts for the 3 h period during which Hurricane Irma made landfall in the Florida Keys (<http://polar.ncep.noaa.gov/waves/index2.shtml>). The wave hindcasts were performed with the third generation WAVEWATCH III spectral wave model (WW3DG et al. 2016). Data from the US East Coast grid used in this study had a 4-arc minute spatial resolution. Wind forcing was from the National Weather Service (NWS) Global Forecasting System (GFS) analysis winds. Conclusions drawn from the wave height model are limited by low spatial resolution (4-arc minute). Thus, the map generated from the model can be used to assess only general east-west differences in wave heights.

2.3.3 Sea Urchin Density and Size Structure

D. antillarum density (urchin m^{-2}) was estimated before and after Hurricane Irma by divers with SCUBA thoroughly searching belt transects (120 m^2 per transect) for individuals under coral heads and reef overhangs, amongst macroalgae, and inside rubble and substrate holes (see Study sites and experimental design). All individuals observed within the belt transects were counted and test diameters were measured with long-jaw calipers to the nearest 1.0 mm. *D. antillarum* population size structure was examined as size frequency distributions of test diameters before and after Hurricane Irma from individuals observed within the belt transects, in addition to individuals encountered

opportunistically adjacent to the transects (to increase sample size for size frequency distributions at low sea urchin abundance). Only counts of individuals within the belt transects were used to determine *D. antillarum* density. Urchins less than 10 mm test diameter size are cryptic and difficult to find (Hunte and Younglao 1988) and therefore may be underreported.

2.3.4 Benthic Community Structure

To examine the impacts of Hurricane Irma on benthic community structure, video was captured along the same belt transects used for *D. antillarum* surveys (see Sea urchin density and size structure) with a GoPro HERO5 camera held by divers swimming approximately 1 m above the bottom. Still images were extracted from each video at a rate of 0.2 images per second to avoid sampling the same area of the reef twice. Using randomly generated numbers, 20 images from each image sequence (out of 30 to 40 images total) were selected for point count analysis in ImageJ (NIH) to estimate average percent cover of benthic organisms within a transect (Aronson et al. 1994). A standardized grid of 50 points was overlaid on each image, and the type of benthic group under each point was categorized. Each image was standardized to an area of approximately 0.7 m x 2.0 m using the transect tape for scale. Benthic groups included hydrocorals, scleractinian corals, dead coral skeleton, sponges, coralline algae, non-coralline calcareous and fleshy brown (e.g. *Dictyota* sp.), green (e.g. *Halimeda* sp.), and red (e.g. *Wrangelia* sp.) macroalgae (hereafter “macroalgae”), turf-algal-sediment matrix (hereafter TAS), sediment, and unknown (e.g. due to an obscured portion of the image). Average percent cover of each benthic group (number of points overlying a group / 50 total points * 100) for the analyzed images was calculated for each transect (n = 20 images per transect). Video was captured on only one belt transect at WS in the middle Keys after Hurricane Irma due to poor visibility (Fig. 2.1).

2.3.5 Statistical Analysis

To examine the effect of Hurricane Irma on *D. antillarum* density (urchin m⁻²), 2-way analysis of variance (ANOVA) was used with ‘Storm’ (fixed factor, 2 levels: before and after the storm) and ‘Location’ (fixed factor, 2 levels: upper and middle Keys) as independent grouping variables. Sites where *D. antillarum* were absent both before and after Hurricane Irma were excluded from the analysis to minimize zero values in the dataset (DS, TR, and PP; Fig. 2.1). The two transects sampled within each site were pooled for the analysis.

To examine whether size frequency distributions of *D. antillarum* test diameters (pooled among sites) differed before (n = 98 urchins) and after (n = 25 urchins) Hurricane Irma, I used the Kolmogorov-Smirnov (K-S) 2-sample test. Test diameter data was not normally distributed (Shapiro-Wilks, p<0.001), so a non-parametric Mann-Whitney U test was used to evaluate differences in median test diameter before and after the storm.

Changes in coral reef community structure following Hurricane Irma were evaluated with 2-way multivariate analysis of variance (MANOVA) on the percent cover of community groups with ‘Storm’ (fixed factor, 2 levels: before and after storm) and ‘Location’ (fixed factor, 2 levels: upper and middle Keys) as independent grouping variables. The unknown category and rare community groups (<1% cover), including

coralline algae (mean percent cover = 0.38%) and dead coral skeleton (mean percent cover = 0.37%), were excluded from the analysis to minimize zero values to meet the assumptions of MANOVA (homogeneity of variances), and because these groups did not contribute substantially to benthic community structure. Following detection of a marginally non-significant interaction in MANOVA (see Results), univariate tests with 2-way ANOVA were conducted for each community group separately with ‘Storm’ (fixed factor, 2 levels: before and after storm) and ‘Location’ (fixed factor, 2 levels: upper and middle Keys) as independent grouping variables. The two transects sampled within each site were pooled for the analyses.

To test for a correlation between sediment transport and *D. antillarum* mortality, I evaluated the relationship between the change in the percent cover of sediment (difference between pre-Irma and post-Irma percent cover) and change in *D. antillarum* density (difference between pre-Irma and post-Irma density) with a non-parametric Spearman’s rank correlation, with transects pooled within sites. Sites where *D. antillarum* were absent before and after Hurricane Irma were excluded from the analysis, given that there was no change in density at these sites (DS, TR, and PP; Fig. 2.1). To test for a correlation between grazer abundance and post-storm algal colonization, Spearman’s rank correlations were also used to investigate the relationship between post-storm *D. antillarum* density (urchin m⁻²) and change in percent cover of macroalgae and TAS, with transects pooled within sites.

Percent cover data were normalized with arcsine transformation prior to the analyses, and normality of transformed data was confirmed using a Shapiro-Wilk test for normality on each community group. The assumption of homogeneity of variances was tested on the transformed percent cover data with a Bartlett test and no violations were detected. All statistical analyses were conducted in R, using the package “dplyr” (Wickham et al. 2018).

2.4 RESULTS

2.4.1 Physical Impacts of Hurricane Irma

Ocean mixing caused by the passage of Hurricane Irma was indicated by a rapid (within 24 hr) 3°C drop in bottom sea temperature, which was consistent at 3 sites spanning the middle and upper Florida Keys (Fig. 2.2). Significant wave heights during landfall of Hurricane Irma from the WAVEWATCH III model indicate that the eye of Hurricane Irma passed directly over the study region, with no clear east-west pattern in wave heights among study sites, and similar magnitudes of waves in the upper and middle Keys (Fig. 2.1).

2.4.2 Sea Urchin Density and Size Structure

There was a significant difference in mean *D. antillarum* density before and after Hurricane Irma (2-way ANOVA: $F_{1,10} = 7.69$, $p = 0.019$), but no effect of ‘Location’ (2-way ANOVA: $F_{1,10} = 0.476$, $p = 0.506$) and no interaction between ‘Storm’ and ‘Location’ (2-way ANOVA: $F_{1,10} = 0.939$, $p = 0.355$). Overall mean density of *D. antillarum* declined from 0.052 urchin m⁻² to 0.014 urchin m⁻² (Fig. 2.3).

Size frequency distributions of test diameters were significantly different before and after Hurricane Irma (K-S test: $p = 0.003$). *D. antillarum* population size structure was dominated by large individuals with 60 to 80 mm test diameter before Hurricane Irma, but shifted to dominance by smaller individuals with 30 to 40 mm test diameter after the storm (Fig. 2.4). Median test diameter was significantly reduced from 65 mm before the storm to 35 mm after the storm (Mann-Whitney U test: $p = 0.0012$).

2.4.3 Benthic Community Structure

Prior to Hurricane Irma, the benthic community at sites in both the middle and upper Keys was dominated by TAS, hydrocorals, sediment, and macroalgae (Fig. 2.5). I observed a marginally non-significant interaction between ‘Storm’ (before and after storm) and ‘Location’ (upper and middle Keys) on benthic community structure (2-way MANOVA: $F_{1,16} = 2.43$, $p = 0.095$; Table 2.2), a marginally non-significant effect of ‘Location’ (2-way MANOVA: $F_{1,16} = 2.43$, $p = 0.096$), and no effect of ‘Storm’ (2-way MANOVA: $F_{1,16} = 1.56$, $p = 0.25$). 2-way ANOVAs indicated that the marginally non-significant interaction was driven by differences in storm impacts on macroalgae in the middle versus upper Florida Keys (2-way ANOVA, Storm x Location: $F_{1,10} = 7.99$, $p = 0.012$; Table 2.3). Examining these locations separately with an a posteriori ANOVA indicates that there was a significant decrease in macroalgae in the middle Keys ($12.6 \pm 5.6\%$ pre-Irma, $6.5 \pm 4.8\%$ post-Irma; ANOVA: $F_{1,12} = 4.8$, $p = 0.049$) and a marginally non-significant increase in macroalgae in the upper Keys ($8.5 \pm 2.2\%$ pre-Irma, $17.9 \pm 7.0\%$ post-Irma; ANOVA: $F_{1,4} = 5.87$, $p = 0.07$) (Table 2.3, Fig. 2.5).

There was no significant interaction between ‘Storm’ and ‘Location’ in the univariate 2-way ANOVA tests for any other community group (Table 2.3). For hydrocorals, there was a significant decrease in percent cover in both the middle ($28.4 \pm 12.7\%$ pre-Irma, $17.4 \pm 13.4\%$ post-Irma) and upper ($24.2 \pm 15.9\%$ pre-Irma, $10.1 \pm 7.4\%$ post-Irma) Keys following the storm (ANOVA: $F_{1,16} = 4.87$, $p = 0.042$; Table 2.3, Fig. 2.5). There was no effect of ‘Location’ on hydrocoral percent cover (Table 2.3). Sponge cover also decreased significantly in the middle ($5.2 \pm 2.8\%$ pre-Irma, $2.5 \pm 1.7\%$ post-Irma) and upper ($1.3 \pm 0.9\%$ pre-Irma, $0.5 \pm 0.3\%$ post-Irma) Keys after the storm (ANOVA: $F_{1,16} = 4.90$, $p = 0.042$; Table 2.3, Fig. 2.5). ‘Location’ had a significant effect on percent cover of sponges (ANOVA: $F_{1,16} = 8.47$, $p = 0.01$; Table 2.3), with a greater percent cover of sponges in the middle Keys as compared to the upper Keys both before and after the storm (Fig. 5). For scleractinian corals, TAS, and sediment, there was no significant effect of either ‘Storm’ or ‘Location’ on percent cover (Table 2.3, Fig. 2.5).

2.4.4 Relationship Between Urchin Abundance and Benthic Community

A Spearman’s rank correlation detected a significant relationship between the change in percent cover of sediment and the change in *D. antillarum* density, with greater decreases in *D. antillarum* density correlating with increased sediment ($R^2 = 0.57$, $p = 0.049$; Fig. 2.6). There was no significant relationship between *D. antillarum* density following Hurricane Irma and the change in percent cover of macroalgae ($R^2 = 0.07$, $p = 0.467$) or TAS ($R^2 = 0.17$, $p = 0.239$).

2.5 DISCUSSION

In the Florida Keys, a reduction in *D. antillarum* density following Hurricane Irma has contributed to a multi-decadal decline of this population due to recurrent disease outbreaks (Forcucci 1994; Kissling et al. 2014). Given the important role of *D. antillarum* as a grazer on Caribbean coral reefs, the lack of recovery of *D. antillarum* following historical disease outbreaks and its continued decline are of great concern for coral reef ecosystem managers (Ladd et al. 2018). My results indicate that recovery of the Florida Keys population is impeded at least in part by strong storms, conditions that are expected to intensify with climate change (Knutson et al. 2010; Cheal et al. 2017). Chronically low *D. antillarum* abundances coupled with increasing frequency of intense storms may diminish the likelihood of local population recovery.

A significant relationship between the increase in sediment percent cover and decline in *D. antillarum* density suggests that sediment transport may have influenced *D. antillarum* mortality through abrasion and burial. Impacts of sediment transport on *D. antillarum* during storms has not previously been reported. However, strong storms can displace large volumes of sediment and deposit it in new locations (Gagan et al. 1990; Hubbard 1992), which can negatively impact benthic reef organisms through tissue damage from sediment suspended in the water column during transport and by physically burying the benthos in a layer of newly deposited sediment (Blair et al. 1994). Alternatively, changes to sediment cover and *D. antillarum* density may be correlated simply due to patterns of water movement during the storm that both resuspended sediments and dislodged urchins due to intense wave action (Verling et al. 2005).

A decrease in median *D. antillarum* test diameter following the storm suggests size-specific mortality that may be related to a lack of structured habitat for large sea urchins on degraded Florida Keys reefs. Smaller *D. antillarum* that are able to seek refuge in reef crevices (Randall et al. 1964) may have been protected from direct sediment abrasion or dislodgement during the passage of Hurricane Irma. Physical structure offered by scleractinian corals is important refuge habitat for juvenile and adult *D. antillarum* (Weil et al. 1984; Lee 2006). However, coral cover was very low at my sites (3% mean cover) and continues to decrease throughout the region due to recent coral disease outbreaks (Walton et al. 2018). Reefs in Southern Mexico, where high survivorship of *D. antillarum* was documented following Hurricane Dean, had greater coral cover than the degraded reefs in my study (12.6% mean cover; Jorgensen et al. 2008), indicating that habitat complexity associated with coral cover may be important for sheltering of *D. antillarum* from storm damage. Coral-depauperate reefs throughout the Caribbean region may offer inadequate refuge habitat to *D. antillarum* due to their increasingly flattened, low-complexity state (Alvarez-Filip et al. 2009), leaving large *D. antillarum* that require proportionately larger refugia more vulnerable to storm damage.

Given that the eye of Hurricane Irma passed through the lower Keys, I expected to observe differences in physical oceanographic conditions between the middle and upper Keys based on their proximity to the storm path. Contrary to this prediction, the hindcast estimates of significant wave heights did not detect a clear difference between locations during the passage of the storm. Similarly, bottom sea temperature data showed a comparable 3°C drop in temperature at 3 sites spanning the study region. These findings are consistent with the lack of a storm by location interaction in ANOVA on *D. antillarum*

density, suggesting that storm impacts on *D. antillarum* were relatively homogenous across a spatial scale of 80 km. This observation is likely due to the overall close proximity of both the middle and upper Keys to the core of the storm (within 120 linear km) and the very high intensity of the storm (Category 4) (Cangialosi et al. 2018).

Spatial variation in storm impacts was evident when comparing changes to the abundance of macroalgae in the middle Keys, where abundance decreased, and upper Keys, where abundance increased. Hurricanes can result in both macroalgal blooms (Woodley et al. 1981; Rogers et al. 1991) and losses (Blair et al. 1994; Mumby et al. 2005) in the Caribbean, and successive changes to the composition of macroalgal species on reefs following hurricane impacts are well-documented (Harmelin-Vivien 1994). My physical oceanographic data and examination of other benthic groups, including *D. antillarum*, indicate that Irma's impacts were similar throughout the middle and upper Keys; therefore it is unlikely that differences in physical storm impacts were a major driver of the observed patterns of macroalgal abundance. Instead, differences in the ability of macroalgae to withstand storm impacts could have influenced post-storm macroalgal abundances. Variation in attachment strength and morphology of different algal species (e.g. weakly attached and erect *Wrangelia* sp.) may influence the composition of algae following a hurricane (Blair et al. 1994). However, initial macroalgal community composition at my sites is not known due to the limitations of image analysis for species-level identification. Bottom-up control of macroalgal abundance (i.e. nutrient availability; Lapointe 1997) also could have influenced the colonization of macroalgae following Hurricane Irma, but changes to nutrient concentrations associated with Irma are not presently known.

Grazing pressure from fish and invertebrate herbivores can also regulate the distribution of macroalgae on reefs following disturbance (Woodley et al. 1981; Carpenter 1986; Hughes 1994). However, I detected no relationship between post-Irma *D. antillarum* density and the change in cover of macroalgae and TAS, indicating that grazing by low densities of *D. antillarum* at my sites was not sufficient to control macroalgal and turf proliferation. Unlike reefs where *D. antillarum* population recovery has resulted in localized decreases in macroalgal abundance (e.g. Edmunds and Carpenter 2001; Idjadi et al. 2010), *D. antillarum* densities at my sites in the Florida Keys remain low, with little sign of population growth (Chiappone et al. 2013). A diverse community of herbivores in addition to *D. antillarum* can be important for regulating algal abundance (Francis et al. 2019), though abundances of other grazers, including other sea urchin species and herbivorous fishes, are not known for my sites.

Although hurricanes have historically contributed to significant losses in the abundance of scleractinian corals throughout the Caribbean, the role of hurricane disturbance in coral decline has waned in recent decades relative to other stressors such as sedimentation and disease (Gardner et al. 2005). Correspondingly, I did not detect an effect of Hurricane Irma on scleractinian coral abundance in my study. The degree of mechanical damage to scleractinian corals can depend on coral morphology, and fragile branching species tend to be more affected by storms than sturdy massive species (Woodley et al. 1981). Since scleractinian coral abundance was initially very low at my sites and the majority of corals were massive species (data not shown), it is unsurprising that overall scleractinian coral abundance was not significantly impacted by Hurricane Irma. However, reports of localized coral mortality following Hurricane Irma, especially in the middle and

lower Keys, indicate that the present study may not fully capture Irma's impacts on scleractinian corals in the region (NOAA 2018).

In the absence of *D. antillarum* grazing to facilitate coral recruitment, the Florida Keys reef ecosystem will likely remain coral-depauperate. Regime shifts between coral- and macroalgal-dominated states are influenced by processes regulating grazing pressure and coral abundance (Mumby 2009), and dramatic increases in grazing intensity or coral recruitment may shift the community towards coral-dominance (Mumby 2007a). Hydrocorals, macroalgae, and TAS dominated the benthic community at my sites prior to Hurricane Irma. Following Irma, the benthic community may remain dominated by relatively fast-growing, soft-bodied community groups including hydrocorals and fleshy macroalgae, which have become increasingly dominant taxa on Florida Keys reefs (Ruzicka et al. 2013). While these soft-bodied benthic groups are commonly susceptible to hurricane damage (Woodley et al. 1981; Hubbard et al. 1991; Blair et al. 1994; Jorgensen et al. 2008), recovery can occur within weeks of storm disturbance following reattachment to substrate and rapid growth (Woodley et al. 1981). These benthic taxa do not provide the complex refuge habitat needed to support *D. antillarum* recruits, which contributes to the habitat limitation that hinders *D. antillarum* population recovery (Miller et al. 2009; Bodmer et al. 2015). Disturbance from strong storms like Hurricane Irma may reinforce the coral-depauperate state by depressing grazing pressure from *D. antillarum* populations during the critical post-storm recovery period, which prevents reestablishment of scleractinian corals and by extension further inhibits *D. antillarum* population recovery.

The scope of the present study is limited to shallow reefs in the middle and upper Keys and the overall status of *D. antillarum* in the Florida Keys remains poorly understood. Large-scale assessments of *D. antillarum* in the Florida Keys are needed to determine the current status of the population. *D. antillarum* abundances may increase locally following Hurricane Irma over timeframes of years as pelagic larvae arrive and recruit to reefs. However, this assumes a source of larvae and post-settlement survival, which can be intermittent and low, respectively (Miller et al. 2009; Feehan et al. 2019). Thus, recovery of *D. antillarum* in the Florida Keys may depend on active management, including mitigating anthropogenic climate change that is driving an increase in storm intensities, and recovering physical reef structure to improve *D. antillarum* survival during storms and provide habitat for recruits.

2.6 TABLES AND FIGURES

Table 2.1. Information about 10 sites sampled in the middle and upper Florida Keys, including site abbreviation, maximum depth, location, and GPS coordinates.

Site Name	Abbreviation	Max. Depth (m)	Location	Coordinates (°N, °W)
Pickles Shallow	PS	3	Upper Keys	24.99098, 80.41495
Pickles Reef	PR	6	Upper Keys	24.99098, 80.41495
Pickles Patch	PP	4.5	Upper Keys	25.01013, 80.45825
Tennessee Patch	TP	5	Middle Keys	24.78316, 80.76324
Tennessee Reef	TR	6	Middle Keys	24.74593, 80.78312
Eleven Foot Mound	EM	6	Middle Keys	24.72371, 80.86186
West Turtle	WT	6	Middle Keys	24.70186, 80.96356
Washerwoman Shallow	WS	3	Middle Keys	24.66456, 81.07415
East Washerwoman	EW	6	Middle Keys	24.66456, 81.07415
Delta Shoal	DS	6	Middle Keys	24.63130, 81.09328

Table 2.2. Two-way multivariate analysis of variance (MANOVA) of the effect of ‘Storm’ (fixed factor, 2 levels: before and after Hurricane Irma), ‘Location’ (fixed factor, 2 levels: upper and middle Keys), and the interaction between ‘Storm’ and ‘Location’ on percent cover (%) of benthic community groups (n = 7 sites middle Keys, 3 sites upper Keys).

Factor	df (num, den)	F-value	p-value
Storm	1, 16	1.56	0.246
Location	1, 16	2.43	0.096
Storm × Location	1, 16	2.43	0.095

Table 2.3. Pre-Irma and post-Irma mean percent cover (% , \pm SD) of benthic community groups in the middle and upper Florida Keys. Also shown are the results of univariate 2-way analysis of variance (ANOVA) of the effect of ‘Storm’ (fixed factor, 2 levels: before and after Hurricane Irma), ‘Location’ (fixed factor, 2 levels: upper and middle Keys), and the interaction between ‘Storm’ and ‘Location’ on percent cover (%) for each community group (n = 7 sites middle Keys, 3 sites upper Keys). **Bold** values are significant at $\alpha = 0.05$.

	Middle Keys		Upper Keys		2-way ANOVA p-value		
	Pre-Irma	Post-Irma	Pre-Irma	Post-Irma	Storm	Location	Storm x Location
Hydrocorals	28.4 (\pm 12.7)	17.4 (\pm 13.4)	24.2 (\pm 15.9)	10.1 (\pm 7.4)	0.042	0.318	0.748
Scleractinian corals	2.9 (\pm 3.2)	3.6 (\pm 5.8)	2.9 (\pm 4.4)	1.0 (\pm 0.9)	0.804	0.651	0.736
Dead coral skeleton	0.3 (\pm 0.3)	0.6 (\pm 0.6)	0.1 (\pm 0.05)	0.2 (\pm 0.2)	--	--	--
Sponges	5.2 (\pm 2.8)	2.5 (\pm 1.7)	1.3 (\pm 0.9)	0.5 (\pm 0.3)	0.042	0.01	0.656
Coralline algae	0.3 (\pm 0.7)	0.3 (\pm 0.6)	0.1 (\pm 0.1)	1.1 (\pm 1.7)	--	--	--
Macroalgae	12.6 (\pm 5.6)	6.5 (\pm 4.8)	8.5 (\pm 2.2)	17.9 (\pm 7.0)	0.359	0.149	0.012
TAS	31.6 (\pm 9.7)	40.9 (\pm 10.3)	39.2 (\pm 17.0)	44.9 (\pm 12.3)	0.120	0.337	0.762
Sediment	17.7 (\pm 6.0)	27.6 (\pm 12.1)	23.3 (\pm 6.9)	24.3 (\pm 7.2)	0.100	0.705	0.348

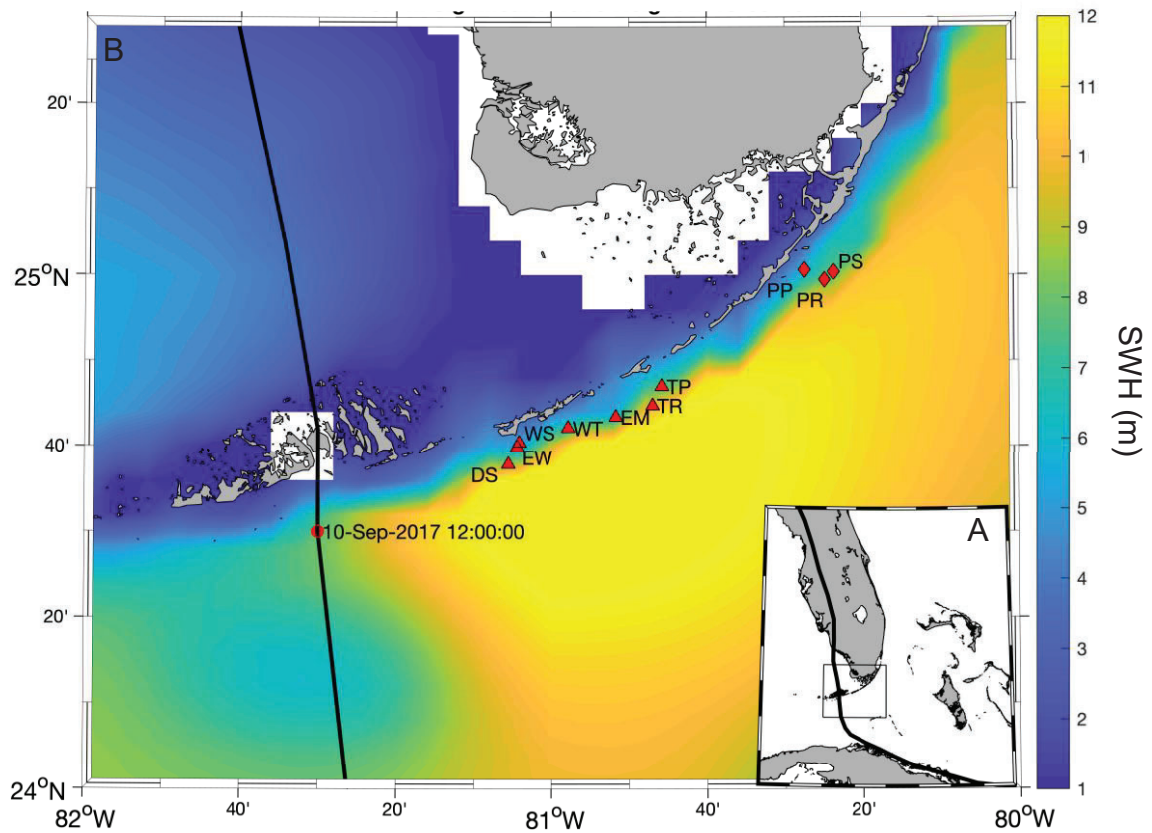


Figure 2.1. Map of the Florida Keys region (A) with inset box (B) showing 10 sites in the middle (red triangles) and upper (red diamonds) Keys sampled to assess storm impacts on *Diadema antillarum* and the surrounding coral reef community. Color contours indicate significant wave heights (SWH, m) from WAVEWATCH III for the 3 h period during which Hurricane Irma made landfall (WW3DG et al. 2016). The solid black lines in A and B indicate the hurricane track.

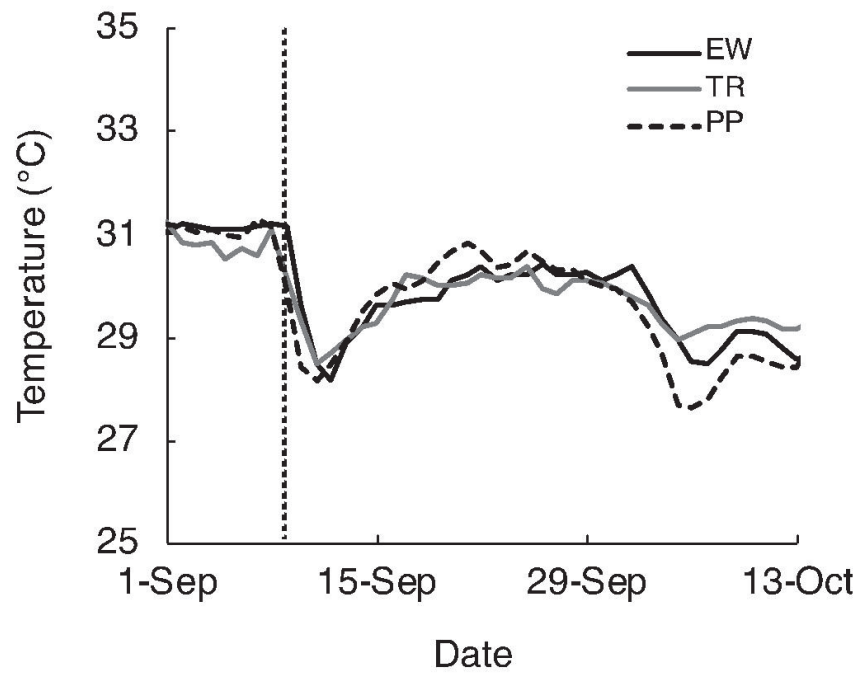


Figure 2.2. Mean daily bottom sea temperature (°C) at 3 sites in the Florida Keys over 6 weeks from 1 September to 13 October 2017. The vertical dashed line indicates when Hurricane Irma made landfall in the Florida Keys. See Fig. 2.1 for site locations.

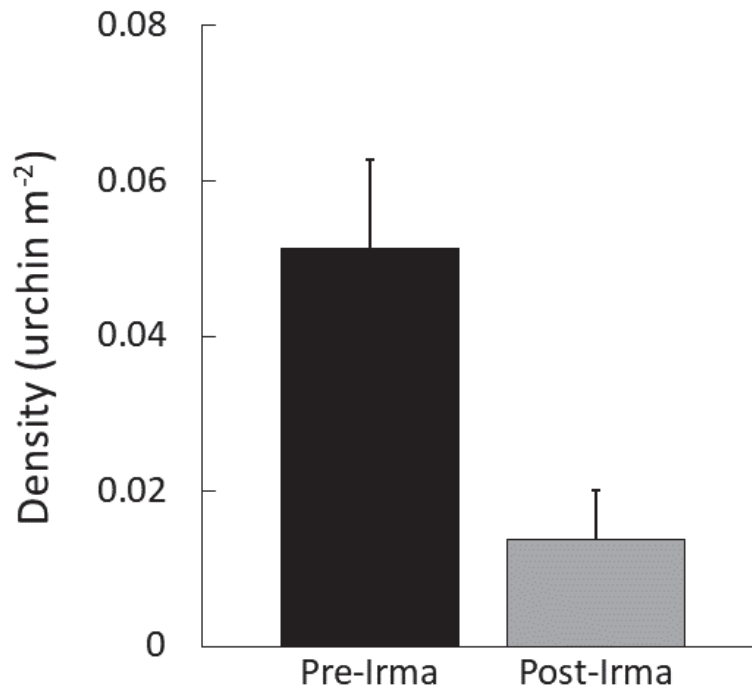


Figure 2.3. Mean density (urchin m⁻²; +SE) of *Diadema antillarum* before and after Hurricane Irma for 7 sites where *D. antillarum* was present before the storm.

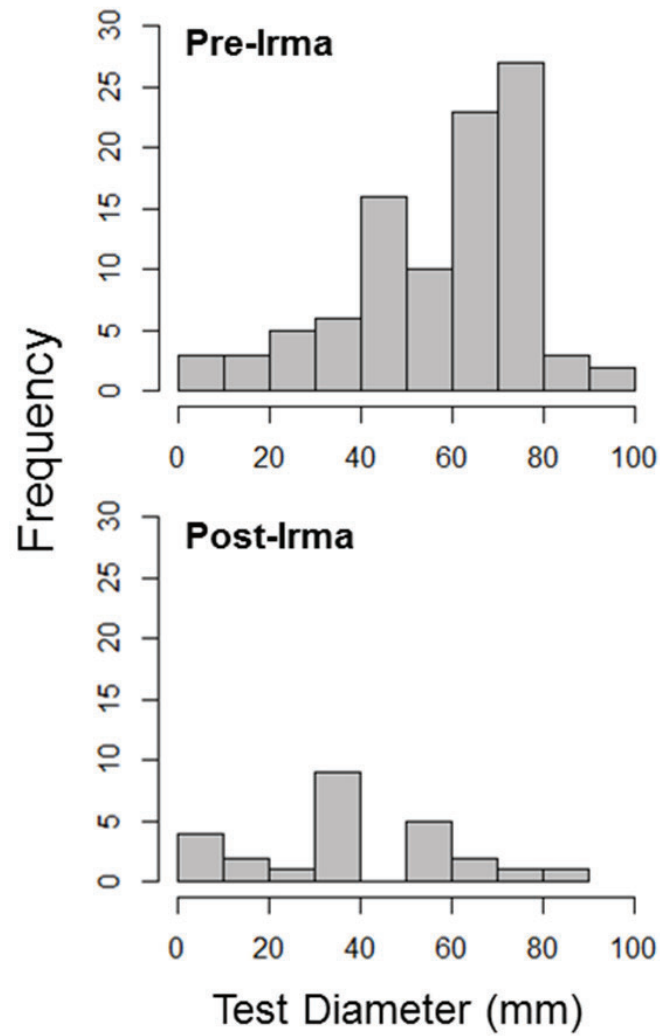


Figure 2.4. Size frequency distributions of *Diadema antillarum* test diameters (mm) at 7 sites in the Florida Keys before (top) and after (bottom) Hurricane Irma (n = 98 urchins pre-Irma, n = 25 urchins post-Irma). A bin size of 5 mm was used to group test diameters.

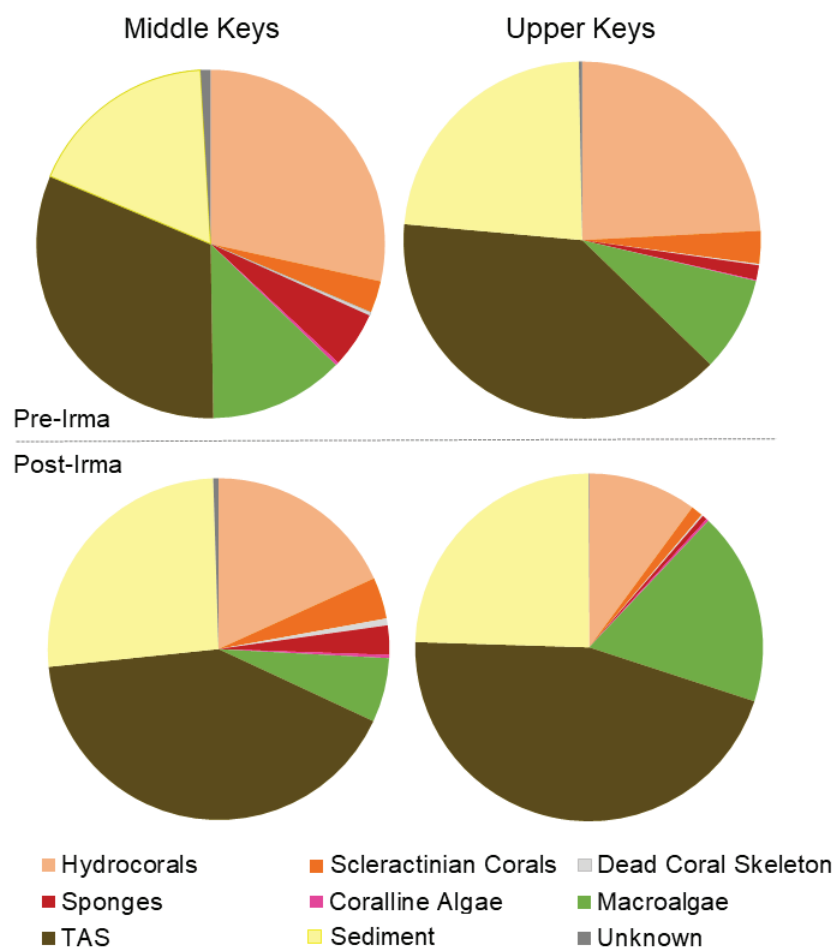


Figure 2.5. Percent cover of benthic community groups (%) before and after Hurricane Irma at sites pooled in the middle and upper Florida Keys ($n = 7$ and 3 sites, respectively). ‘TAS’ is turf-algal-sediment matrix. ‘Unknown’ indicates that the community group could not be identified.

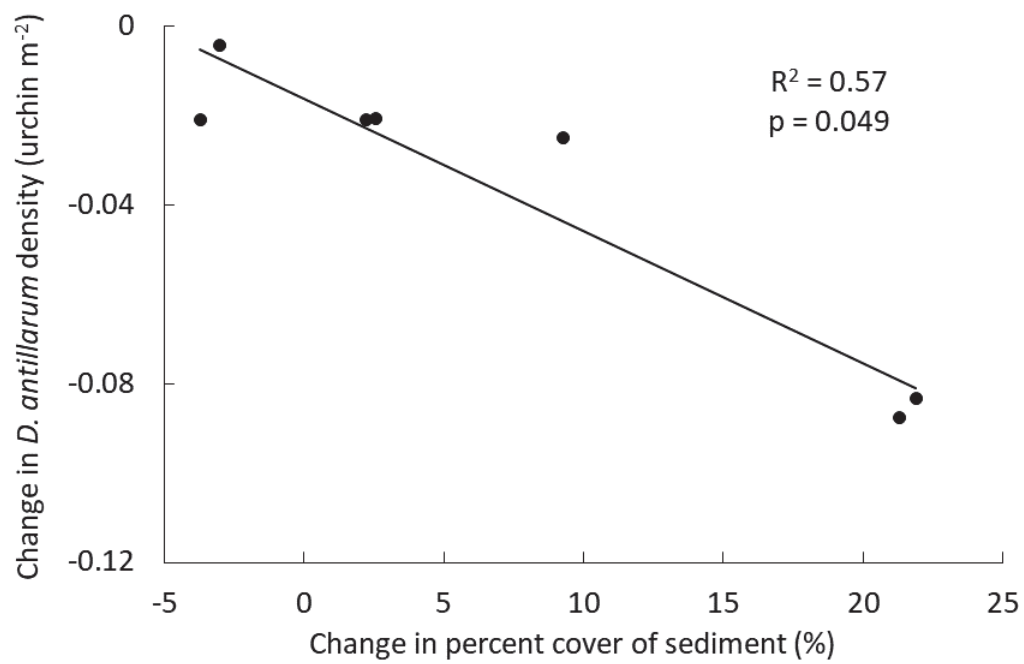


Figure 2.6. Relationship between the change in *Diadema antillarum* density (urchin m⁻²) and change in percent cover of sediment (%) at 7 sites in the Florida Keys. The Spearman's rank correlation R² value and p-value, and regression line ($y = -0.003x - 0.0161$) are shown.

CHAPTER 3

LARVAL INFLUX OF *DIADEMA ANTILLARUM* FOLLOWING DISTURBANCE: INSIGHTS INTO SLOW POPULATION RECOVERY IN THE FLORIDA KEYS

3.1 ABSTRACT

Following population declines due to epidemics and hurricanes, *Diadema antillarum* recovery in the Florida Keys may be hindered by limited influx of new individuals into the population. To test this hypothesis, I analyzed *D. antillarum* larval influx on Astroturf settlement collectors at sites in the Florida Keys before and after a disturbance event (Hurricane Irma). To investigate whether the disturbance event altered local availability of larvae, I measured larval influx on settlement collectors post-storm for comparison with baseline data collected before the storm. I also related larval influx measurements following the storm to spatial patterns of adult density 18 months post-storm to determine whether larval influx has yielded population recovery. The results indicate that larval availability was not significantly affected by the storm, suggesting a distant, external source of larvae rather than local recruitment. Following the storm, there was variation in larval influx among sites, with a trend of higher larval influx at offshore reefs than inshore reefs. However, higher larval abundance offshore did not result in a greater population density. This phenomenon of decoupling between the abundance of larval and adult *D. antillarum* suggests that inshore reefs may be mainly limited by low larval supply, while offshore reefs are limited by high post-settlement mortality.

3.2 INTRODUCTION

The complex life history of *D. antillarum* includes dioecious broadcast spawning of benthic adults followed by a planktonic larval stage lasting 4 to 6 weeks, which can allow for significant larval dispersal and population connectivity (Eckert 1998). Metamorphosis and settlement onto the benthos are induced by environmental cues once larvae are considered “competent” and juvenile features have developed within the larva (Hadfield and Paul 2001), though specific settlement cues have yet to be identified for *D. antillarum*. *D. antillarum* reproductive dynamics are density-dependent and current population densities in the Florida Keys are likely below the threshold to achieve high fertilization success necessary for self-seeded recovery (Feehan et al. 2016). Despite the fertilization limitation of the Florida Keys population, *D. antillarum* larval influx to settlement collectors in the Florida Keys was observed in association with an intermittent oceanographic event (passage of a mesoscale eddy), suggesting that larvae are supplied from an external source population that experiences relatively high reproductive success (Feehan et al. 2019).

Although occasional settlement pulses are evident from the presence of cohorts of small *D. antillarum* on some reefs in the Florida Keys, the population has been relatively stable at low densities following two epidemics in the past several decades, with no indication of regrowth (Chiappone et al. 2002, 2013). Population growth could be limited by processes affecting early life stages including low larval supply and high post-settlement mortality (Chiappone et al. 2002; Miller et al. 2009). Several studies suggest that larval

supply is low in the Florida Keys relative to other *D. antillarum* populations and an inverse relationship exists between adult and larval densities at inshore and offshore reefs (Miller et al. 2009; Feehan et al. 2019). Similar to the Florida Keys, offshore reefs in Puerto Rico receive a high larval supply relative to inshore reefs, while adult *D. antillarum* are more abundant inshore than offshore (Williams et al. 2010). These mismatches between *D. antillarum* larval influx and adult densities suggest that post-settlement mortality may offset larval supply on some reefs and limit population recovery (Williams et al. 2010; Rogers and Lorenzen 2016).

D. antillarum population densities declined by 80% at sites in the Florida Keys following Hurricane Irma in September 2017 (see Chapter 2). The reestablishment of *D. antillarum* at these sites will depend on an influx of new individuals into the population, including the arrival of competent larvae, successful settlement onto reefs, and post-settlement survival to adulthood. This chapter aims to assess *D. antillarum* larval influx onto reefs in the Florida Keys as an indication of population recovery potential. Given previously reported inshore-offshore patterns of larval influx (Williams et al. 2010; Feehan et al. 2019), I expected to observe an inshore-offshore pattern of recovery following Hurricane Irma related to differences in larval influx. I examined *D. antillarum* larval influx before and after Hurricane Irma to determine whether the availability of larvae on Florida Keys reefs was affected by Hurricane Irma due to the local declines in reproductive populations. I then analyzed inshore-offshore spatial patterns in *D. antillarum* larval influx and subsequent changes in benthic adult abundances to determine whether influx of larvae is yielding population recovery.

3.3 METHODS

3.3.1 Study Sites

Population recovery following the impacts of Hurricane Irma on *D. antillarum* was assessed by measuring adult *D. antillarum* densities at 10 sites (3 to 6 m max. depth) including inshore patch reefs (n = 6 sites) and offshore bank-barrier reefs or rubble reef flats (n = 4 sites) spanning 80 km (linear distance) in the upper and middle Florida Keys (Fig. 3.1; see Chapter 2, Table 2.1 for site data).

D. antillarum larval influx was assessed at a subset of the 10 sites, in three regions spanning of the middle and upper Florida Keys. Each region contained two paired sites: one inshore patch reef and one offshore bank-barrier reef (4 to 6 m max. depth) for a total of 6 sites (O1, O2, O3, I1, I2, I3; Fig. 3.1). To characterize physical differences between sites where larval influx was monitored, water temperature data was collected at each site at 2 m above the seafloor from January 25, 2018 to June 6, 2018 with HOBO Pendant® Temperature/Light 8K data loggers (1-h interval) attached to concrete blocks placed adjacent to the reef. Time series of mean daily temperatures were plotted for inshore (n = 3 sites) and offshore (n = 3 sites) locations (Fig. 3.2)

3.3.2 Storm Impacts on Sea Urchin Larval Influx

Larval influx was measured on Astroturf settlement plates at two sites (O1 and I1; Fig. 3.1) during 17 months before (August 2015 to August 2017) and 11 months after

(January to November 2018) Hurricane Irma (September 2017) to examine *D. antillarum* larval availability. Astroturf settlement plates can be successfully used to approximate the influx of competent *D. antillarum* larvae reaching a reef, since larvae readily settle and metamorphose onto this substrate (Williams et al. 2010, 2011). Since larval densities in the water column were not sampled and abundances of newly settled *D. antillarum* were not measured on natural reef substrate, the abundance of settlers on a plate can only be used as a measure of relative abundances of competent larvae among locations. Settlement plates from August 2015 to August 2017 were deployed and processed by Florida Fish and Wildlife Research Institute (FWRI) and C.J. Feehan. Sporadic gaps in settlement monitoring at sites during May 2016, December 2016 to June 2017, and September 2017 to December 2017 occurred due to logistical constraints, including displacement of plates by Hurricane Irma.

Individual settlement plates (0.12 x 0.18 m; height x width) were attached at two depths (2.0 m and 0.2 m above bottom) on two replicate buoyed lines secured to a concrete block placed on sand bottom adjacent to reef habitat at each site (four plates total per site) (Fig. 3.3). Plates were placed at two depths to increase the likelihood of collecting competent larvae, including those within the water column (2.0 m) and those that have settled to the benthos (0.2 m). Plates were collected and replaced monthly to allow time for settlers to accumulate, but reduce potential effects of post-settlement mortality (Williams et al. 2011). Following collection, plates were preserved in ethanol, rinsed through a 150 μ m nylon filter, and the contents of the filtered material was inspected under a dissecting microscope in the lab to enumerate settlers (< 1 mm test diameter, Williams et al. 2010). Counts of *D. antillarum* settlers were standardized into densities (ind. m⁻² of settlement plate) for data visualization to facilitate comparison with other *D. antillarum* settlement studies (Miller et al. 2009; Williams et al. 2010).

3.3.3 Spatial Patterns of Adults and Linkages to Larval Influx

To assess population recovery following Hurricane Irma, adult *D. antillarum* densities were measured at 10 onshore and offshore sites during 3 sampling periods (Fig. 3.1). Adult *D. antillarum* densities measured in March 2019 (18 months following Irma) were compared to density data collected before (June and August 2017) and immediately after (November 2017) the storm (see Chapter 2). In 2017, densities were measured within two 60 x 2 m belt transects placed 10 m apart in an east-west orientation at each site (120 m² of reef surveyed per transect). Densities were measured using the same methods in 2019, but slightly shorter transects (50 x 2 m belt transects, 100 m² of reef surveyed per transect) were employed due to time constraints, which could have resulted in underreporting of urchin abundances during this sampling period. Transects were thoroughly searched by divers with SCUBA for *D. antillarum* present under coral heads and reef overhangs, within macroalgae, and inside rubble and substrate holes. All individuals observed within the belt transects were counted and test diameters measured with long-jaw calipers to the nearest 1.0 mm. Test diameter measurements were used to generate size-frequency histograms for March 2019 to assess abundances of juveniles (<25 mm test diameter; Levitan 1991) that likely settled within the last few months and compare population size (age) structure between locations. Urchins encountered outside of a transect

at a site were opportunistically measured (test diameter, mm), but not included in the density estimates.

To link patterns of population recovery to associated larval influx, a subset of the sites were examined for monthly larval influx. Over 11 months from January 2018 to November 2018, monthly larval influx was measured at a subset of 3 inshore (I1, I2, I3) and 3 offshore (O1, O2, O3) sites on settlement plates at 2 depths (0.2 and 2.0 m; 4 plates per site) using the methods described above (see 3.3.2 Storm Impacts on Sea Urchin Larval Influx) (Fig. 3.1).

3.3.4 Statistical Analysis

Prior to analysis, the assumptions of normality and homogeneity of variances for parametric statistics were evaluated with Shapiro-Wilks test and Bartlett's test, respectively. All statistical analyses were completed in R and Statistica ($\alpha = 0.05$).

Effects of Hurricane Irma on larval availability in the Florida Keys were evaluated by examining monthly settlement counts at two sites (O1 and I1) before ($n=17$ months) and after ($n=11$ months) the storm. Count data did not meet the assumptions of analysis of variance (ANOVA; i.e. homogeneity of variances), so non-parametric tests were employed. Two random factors (Site, 2 levels: I1 and O1; Depth, 2 levels: 0.2 m and 2.0 m) were evaluated separately for differences in monthly settlement with a Mann-Whitney U test. Depth was found to be non-significant (Mann-Whitney U, $p=0.613$), and therefore depths were pooled for further analysis. Site was found to be significant (Mann-Whitney U: $p=0.015$), so each site was analyzed separately to evaluate storm effects. Plates on replicate buoyed lines were pooled for the analysis.

The recovery of *D. antillarum* on reefs was assessed by comparing adult densities (ind. m^{-2}) on transects ($n = 2$ transects per site) at 10 sites among sampling dates (pre-storm, immediately post-storm, and 18 months post-storm) and between locations (inshore and offshore). Density data did not meet the assumptions of ANOVA (homogeneity of variances), so non-parametric tests were employed. The random factor of site was found to be non-significant for each combination of location and date (Kruskal-Wallis: $p>0.05$) so sites were pooled for further analysis. A Mann-Whitney U test was used to evaluate significant differences between *D. antillarum* densities at inshore ($n = 12$ transects) and offshore ($n = 8$ transects) locations for each sampling date separately. A Kruskal-Wallis test was used to evaluate significant differences in adult *D. antillarum* densities between sampling dates for inshore sites and offshore sites separately. A non-parametric Kolmogorov-Smirnov 2-sample test was used to evaluate differences between test diameter size frequency distributions at inshore and offshore locations for benthic *D. antillarum* measured in March 2019.

To test for the presence of an inshore-offshore pattern of larval influx, monthly settlement counts ($n = 11$ months) at six sites (O1, O2, O3, I1, I2, I3) following the storm were compared. Count data did not meet the assumptions of ANOVA (homogeneity of variances), so non-parametric tests were employed. The random factors of site (6 levels: I1, I2, I3, O1, O2, O3) and depth (2 levels: 0.2 m and 2.0 m) were evaluated with a Kruskal-Wallis test and a Mann-Whitney U test, respectively. Depth was found to be a non-significant factor (Mann-Whitney U: $p=0.701$), and therefore depths were pooled for further analysis. A significant effect of site was found for the offshore location (Kruskal-

Wallis: $p=0.013$), but nonparametric post-hoc tests indicate highly nonsignificant ($p > 0.25$) or marginally nonsignificant ($p < 0.10$) differences among the combinations of offshore sites. No difference was detected among inshore sites (Kruskal-Wallis: $p=0.368$); therefore sites were pooled to test for an inshore-offshore effect with a Mann-Whitney U test.

3.4 RESULTS

3.4.1 Water Temperature

Mean daily water temperatures at inshore sites ($n = 3$) and offshore sites ($n = 3$) were similar, but differed by up to 1°C on several occasions, with inshore sites exhibiting greater temperature variability (higher temperature maxima and lower temperature minima) (Fig. 3.2).

3.4.2 Storm Impacts on Sea Urchin Larval Influx

Monthly settlement patterns show sporadic settlement pulses at I1, and more consistent settlement at O1 through time (Fig. 3.4A). There was no significant difference in monthly settlement before and after Hurricane Irma at site I1 (Mann-Whitney U: $p=0.796$) or O1 (Mann-Whitney U: $p=0.118$) (Fig. 3.5).

3.4.3 Spatial Patterns of Adults and Linkages to Larval Influx

Differences in inshore and offshore adult *D. antillarum* density were nonsignificant before Hurricane Irma (Mann-Whitney U: $p=0.091$), with a pattern of higher density inshore than offshore (Fig. 3.6). There was no significant difference in density at inshore and offshore locations after Hurricane Irma in 2017 (Mann-Whitney U: $p=1.0$) or 2019 (Mann-Whitney U: $p=0.394$). At the inshore location, there was a significant difference in *D. antillarum* density among sampling dates (Kruskal-Wallis: $p=0.027$). Post-hoc analysis revealed that density before Irma was significantly different than density after Irma in 2017 ($p=0.022$), but density in 2019 did not significantly differ from either pre-Irma ($p=0.235$) or post-Irma ($p=0.272$) 2017 sampling dates. There was no significant difference in density at offshore sites through time (Kruskal-Wallis: $p=0.897$). Only one juvenile (test diameter < 25 mm; Levitan 1991) was found at each location in 2019. Overall size frequency distributions of the two populations were significantly different between locations (Kolmogorov-Smirnov: $p= 0.012$) (Fig. 3.7). There was a significant effect of location on monthly settlement of *D. antillarum* larvae (Mann-Whitney U: $p<0.001$), with offshore sites experiencing higher monthly settlement than inshore sites (Fig. 3.8). Monthly settlement patterns through time show consistent settlement at offshore sites, and a single settlement pulse during one month at inshore sites during 2018 (Fig. 3.4B).

3.5 DISCUSSION

Understanding the ecological processes linking pelagic larvae and benthic adults can be important for predicting population growth following disturbance. Supply-side

ecology proposes that variation in larval settlement can be a major driver of the structure of benthic assemblages (Lewin 1986; Underwood and Fairweather 1989), although post-settlement mortality or migration may contribute to a mismatch between larval, juvenile, and adult distributions (Hunt and Scheibling 1997). In my study, I found that while disturbance from Hurricane Irma decreased the abundance of *D. antillarum* in the Florida Keys, these losses did not result in reduced availability of pelagic larvae. This suggests that the population still has potential for recovery via an influx of new individuals, provided that adequate larval supply can result in successful recruitment onto reefs.

Spatial variation in settlement abundances can be driven by pre-settlement processes including hydrodynamic forces, environmental conditions, and larval behavior (Rodriguez et al. 1993). Larvae arriving in the Florida Keys are likely from an external source, given the metapopulation dynamics of *D. antillarum* throughout the Caribbean (Karlson and Levitan 1990) and low fertilization success experienced locally (Feehan et al. 2016). Given that larval influx was not affected by local losses in adult *D. antillarum* densities following Hurricane Irma, the results support the hypothesis that larvae arriving in the Florida Keys are produced from an external source. *D. antillarum* larval supply to the Florida Keys may be linked to local mesoscale eddy activity, which is hypothesized to entrain larvae from an upstream source and disperse them onto Florida Keys reefs (Feehan et al. 2019). *D. antillarum* larvae may arrive at offshore reefs first, then decrease in concentration as they are transported further inshore, either through settlement onto reefs or mortality from planktivorous predators (Williams et al. 2011), resulting in low larval influx at inshore sites. Water temperature differences between sites may also influence larval survival and settlement. Though temperature differences between inshore and offshore sites were not drastic, on several occasions mean daily water temperatures at inshore sites diverged from offshore sites by up to 1°C higher or lower than offshore sites (Fig. 3.3). *D. antillarum* larvae may be sensitive to high temperature (Eckert 1998) and it is possible that larvae had higher survival at offshore sites, where temperatures were less variable. Larval densities, rather than post-settlement mortality, may be limiting population growth at inshore reefs where *D. antillarum* persist despite low larval abundances.

My analysis detected an inshore-offshore spatial pattern in *D. antillarum* larval supply that did not match spatial patterns of population density. Maximum larval supply at inshore sites ($\text{max} = 20 \text{ ind. m}^{-2} \text{ month}^{-1}$) is higher than values reported in previous studies in the Florida Keys ($\text{max} < 2 \text{ ind. m}^{-2} \text{ month}^{-1}$; Miller et al. 2009). However, this pulse of larval influx occurred during only one month at one site (I1; Fig 3.4B), and settlement was absent during all other months at all inshore sites, indicating generally low larval supply to inshore reefs. In contrast, larval supply at offshore sites ($\text{max} = 45 \text{ ind. m}^{-2} \text{ month}^{-1}$) was relatively high, intermediate to values previously reported at offshore sites in the Florida Keys ($\text{max} 23 \text{ ind. m}^{-2} \text{ month}^{-1}$, Feehan et al. 2019) and Puerto Rico ($\text{max} 16 \text{ ind. m}^{-2} \text{ month}^{-1}$; Miller et al. 2009, $\text{max} 265 \text{ ind. m}^{-2} \text{ month}^{-1}$; Williams et al. 2011). Still, settlement at both locations was much lower than pre-mortality estimates of *D. antillarum* settlement in Curaçao ($\text{max} 376 \text{ ind. m}^{-2} \text{ month}^{-1}$; Bak 1985).

While there is some evidence for *D. antillarum* population recovery at the sites, 2019 and pre-Irma densities were not significantly different, indicating that increases in the *D. antillarum* population density were small and occurred mostly at inshore sites where little to no larval influx was detected. This pattern suggests that different processes may influence *D. antillarum* population dynamics at inshore and offshore locations. It is

important to note that the Astroturf settlement plates used in this study have an unknown lower limit of detection of larvae. Indeed, the results of this study may in general be limited by the low detectability of rare species and cryptic early life stages. Accurate population assessments of rare species with patchy distributions typically require substantial sampling effort through space and time (MacKenzie et al. 2005). In addition, detectability of newly settled juveniles (<10 mm) is low because small individuals are cryptic and tend to hide deep within reef crevices (Hunte and Younglao 1988).

Due to the poorly understood seasonal (Forcucci 1994) and ontological (Lewis 1966) variation in *D. antillarum* test diameter growth (2 to 7 mm month⁻¹; Randall et al. 1964; Bauer 1976), it is difficult to accurately assess recruitment onto reefs with infrequent size-frequency sampling. If post-settlement mortality were constant between locations, I would expect reefs with higher larval supply to have higher recruitment and higher abundances of adults (López et al. 1998). However, high larval supply has not resulted in major population growth at offshore sites, where densities remain low, suggesting a population bottleneck at either the settlement or post-settlement stage.

Prior to Hurricane Irma, there was a pattern of higher adult *D. antillarum* densities at inshore sites than offshore sites (Fig 3.5A), which is supported by previous observations in the Florida Keys (Miller et al. 2009). This spatial pattern was lost following hurricane disturbance (Fig 3.5B) and has not yet been reestablished (Fig 3.5C). Trends at the inshore and offshore locations suggest that the spatial pattern may return in time. Similar abundances of juveniles were found at both sites, but inshore sites appear to support more large individuals (>60 mm test diameter) than offshore sites (Fig 3.6). The absence of large individuals at offshore sites suggests that offshore reefs are poor habitat for adult *D. antillarum*. Newly settled *D. antillarum* can experience substantial mortality from predation or physical disturbance (Randall et al. 1964) and *D. antillarum* populations are often considered recruitment-limited due to high post-settlement mortality (Karlson and Levitan 1990; Bodmer et al. 2015). Complex habitat that provides refuge from predation is important for the survival of juvenile sea urchins (Clemente et al. 2013; Yiu and Feehan 2017), and physical structure offered by hard, reef-building corals (Scleractinia) is important refuge habitat for juvenile and adult *D. antillarum* (Weil et al. 1984; Lee 2006). Local abundances of predators have not been measured at my sites, but coral cover is known to be generally low in the Florida Keys (Schutte et al. 2010) and is decreasing due to recent coral disease outbreaks throughout the region (Walton et al. 2018).

This study examined a pattern of decoupling between *D. antillarum* larval supply and benthic adults that has been previously reported in the Florida Keys (Feehan et al. 2019) and Puerto Rico (Williams et al. 2010, 2011). In these regions, post-settlement processes may regulate *D. antillarum* densities at offshore sites, while larval supply may limit densities at inshore sites. In contrast, Rogers and Lorenzen (2016) documented higher *D. antillarum* settlement at back reef (inshore) sites than forereef (offshore) sites in Curacao, but settlement densities were not correlated to adult densities. Several decades ago in other regions of the Caribbean, density-dependent recruitment was thought to drive *D. antillarum* population dynamics, where adult distribution matched the distribution of early life stages (Bak 1985; Hunte and Younglao 1988). *D. antillarum* population dynamics may have been altered as Caribbean coral reef ecosystems have changed in recent decades.

D. antillarum in the Florida Keys are still in the early stages of recovery from a major disturbance event, Hurricane Irma (see Chapter 2), evidenced by limited re-

establishment of *D. antillarum* on several reefs examined in this study. I did not detect a significant inshore-offshore spatial pattern of recovery, which may be due to slow rates of population growth and low detectability of benthic adults. *D. antillarum* population re-establishment can be rapid following disturbance (within a year), provided there is adequate larval supply and recruitment success (Hunte and Younglao 1988). However, in the Florida Keys, population recovery may be limited by a combination of relatively low larval supply and high post-settlement mortality on degraded reefs. While recovery to pre-Irma densities may be possible, it is unclear whether *D. antillarum* will be able to recover to pre-disease densities and restore their essential function as keystone herbivores on coral reefs.

3.6 FIGURES

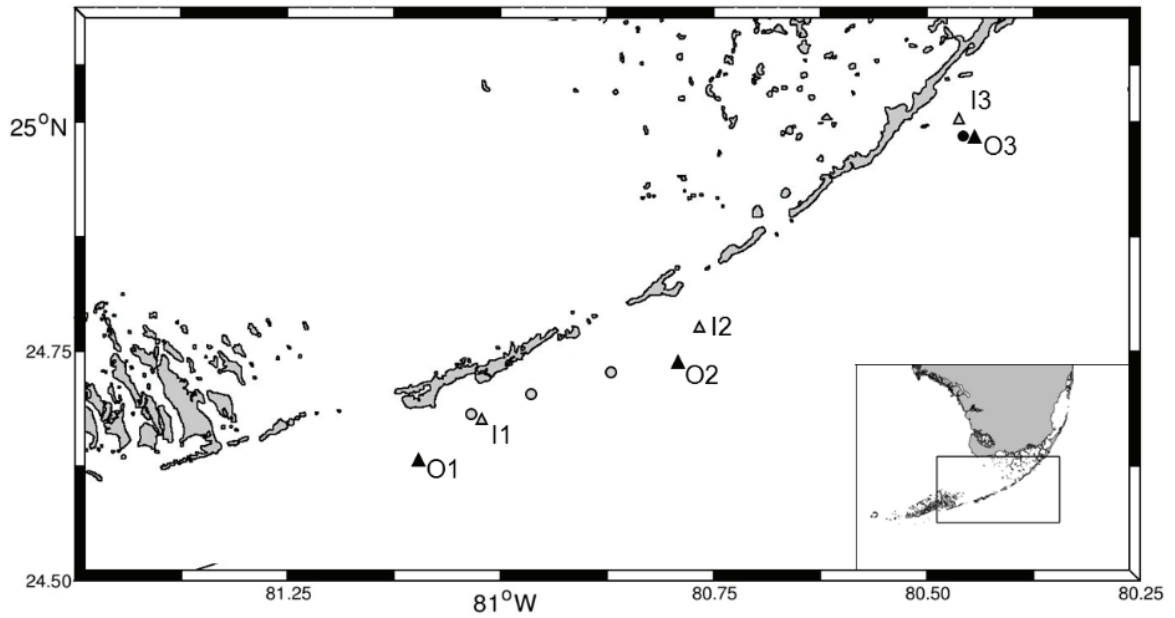


Figure 3.1. Map of southern Florida with inset showing inshore patch reefs (grey) and offshore bank-barrier reefs or rubble reef flats (black) in the Florida Keys where benthic *Diadema antillarum* abundances were measured (both circles and triangles). *D. antillarum* larval influx was assessed with settlement plates at a subset of paired inshore (I1, I2, I3) and offshore (O1, O2, O3) sites (triangles).

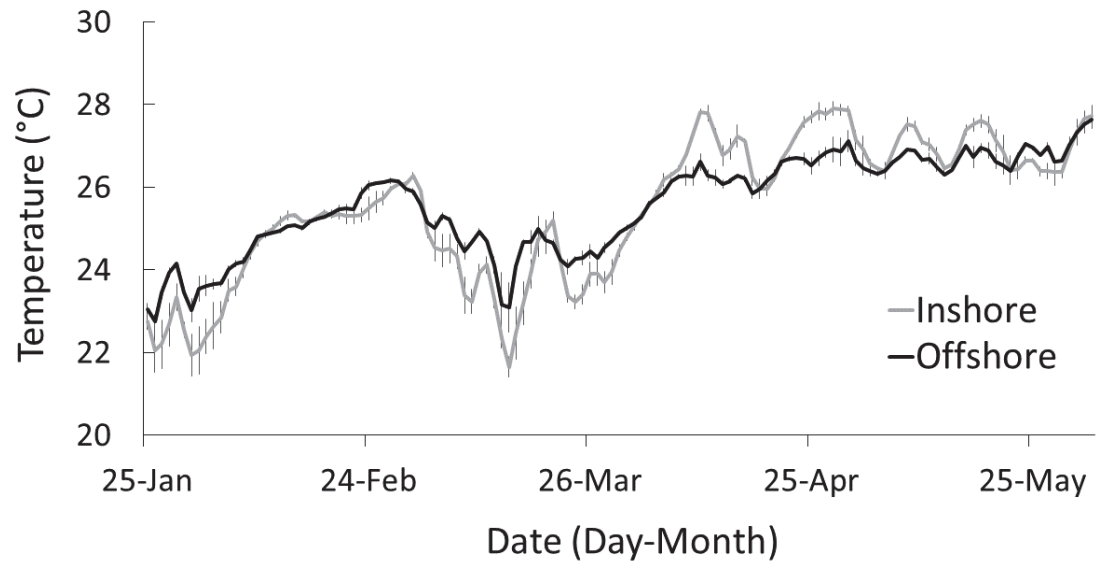


Figure 3.2. Mean daily sea temperature (+SE) at 2 m above bottom at inshore ($n = 3$) and offshore ($n = 3$) sites from January 25 to June 2, 2018 measured with HOBO temperature loggers (1-h interval data).

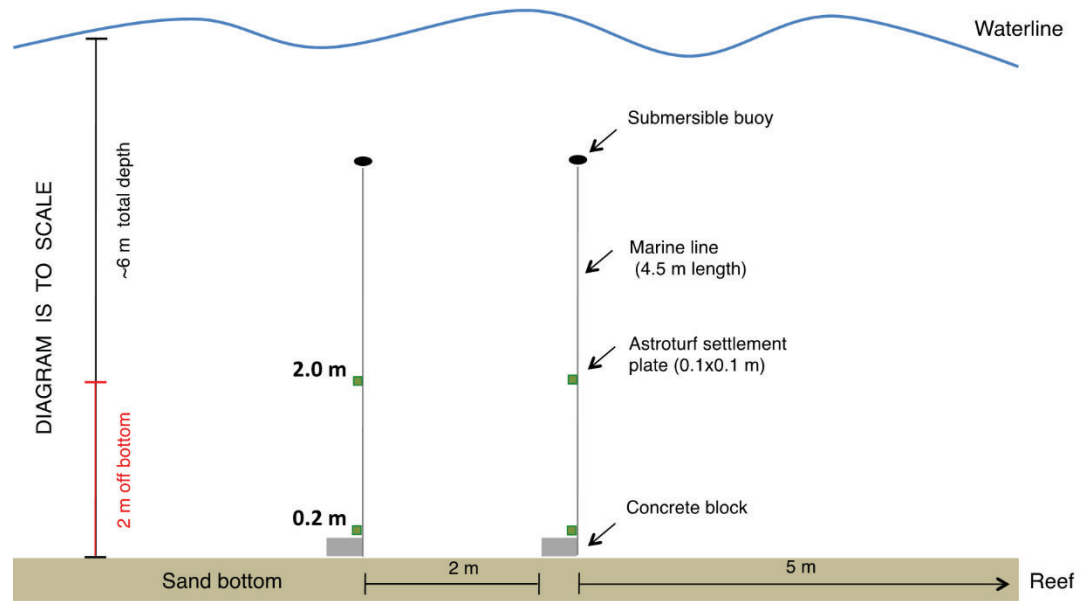


Figure 3.3. Diagram of Astroturf settlement collectors used to assess *Diadema antillarum* larval influx to reefs in the Florida Keys. Adapted from C. J. Feehan, SWG Proposal (2016).

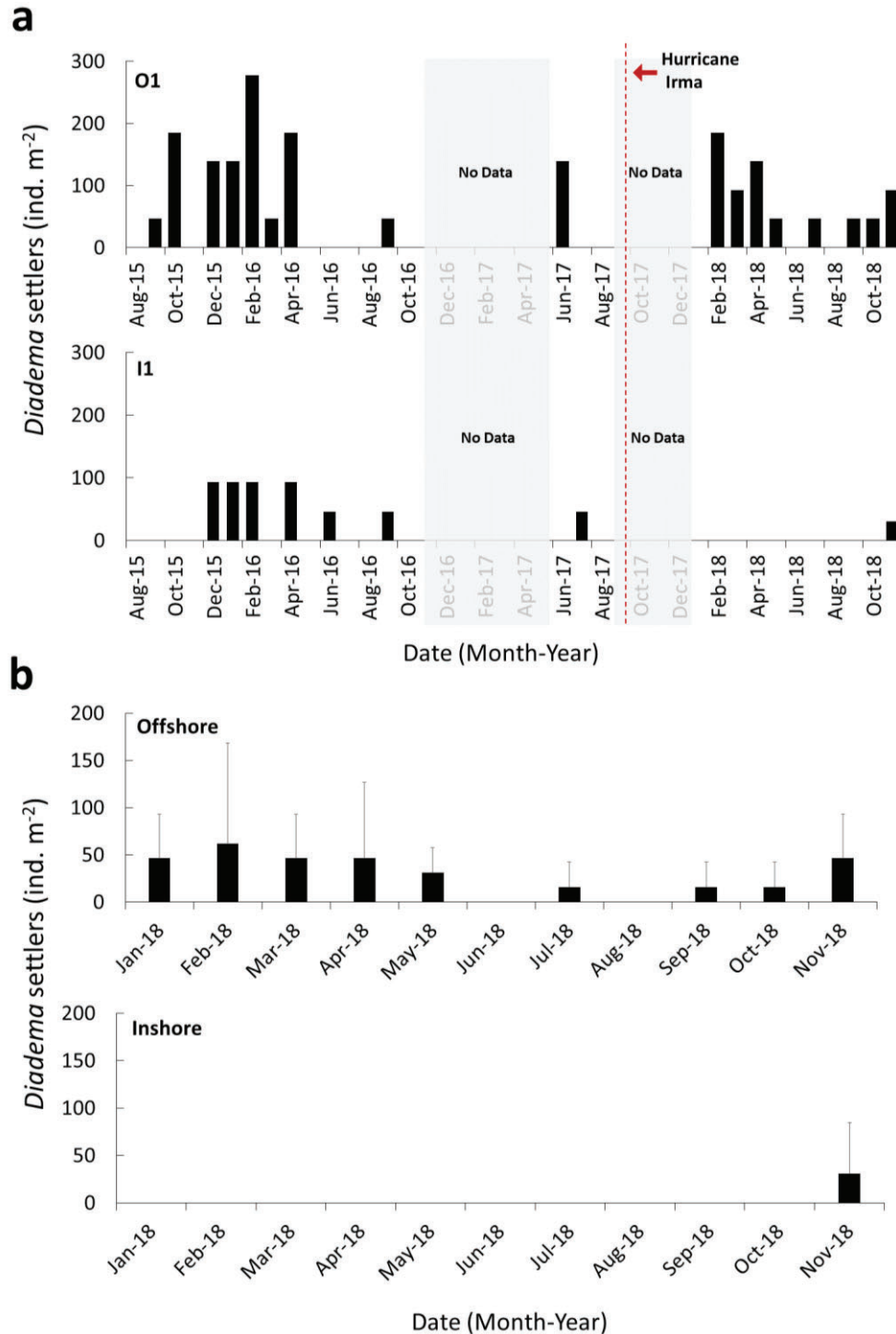


Figure 3.4. *Diadema antillarum* settlement over time for (a) two sites (O1 and I1) in the Florida Keys, showing monthly settlement patterns before and after Hurricane Irma. Grey boxes show months with no settlement data, and vertical dashed red line indicates the passage of Hurricane Irma (September 10, 2017). Also shown is mean monthly settlement (mean + SE) over time (b) for offshore (n=3) and inshore (n=3) sites in the Florida Keys in 2018.

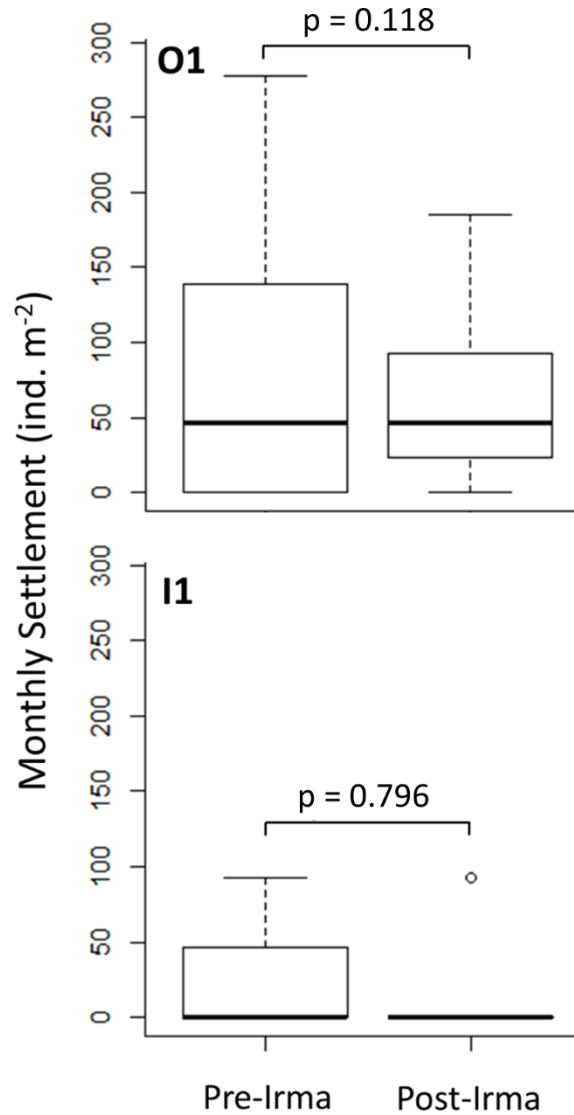


Figure 3.5 Pre-hurricane (n=17 months) and post-hurricane (n=11 months) monthly *Diadema antillarum* larval settlement at sites O1 (top) and I1 (bottom) in the Florida Keys (p-values of Mann-Whitney U tests are shown). In the box plots, horizontal box boundaries show the 25th (lower) and 75th (upper) percentiles, bold horizontal bars within the box shows median monthly settlement, whiskers show maximum (above) and minimum (below) values, and points above the boxes show outliers outside the 90th percentile.

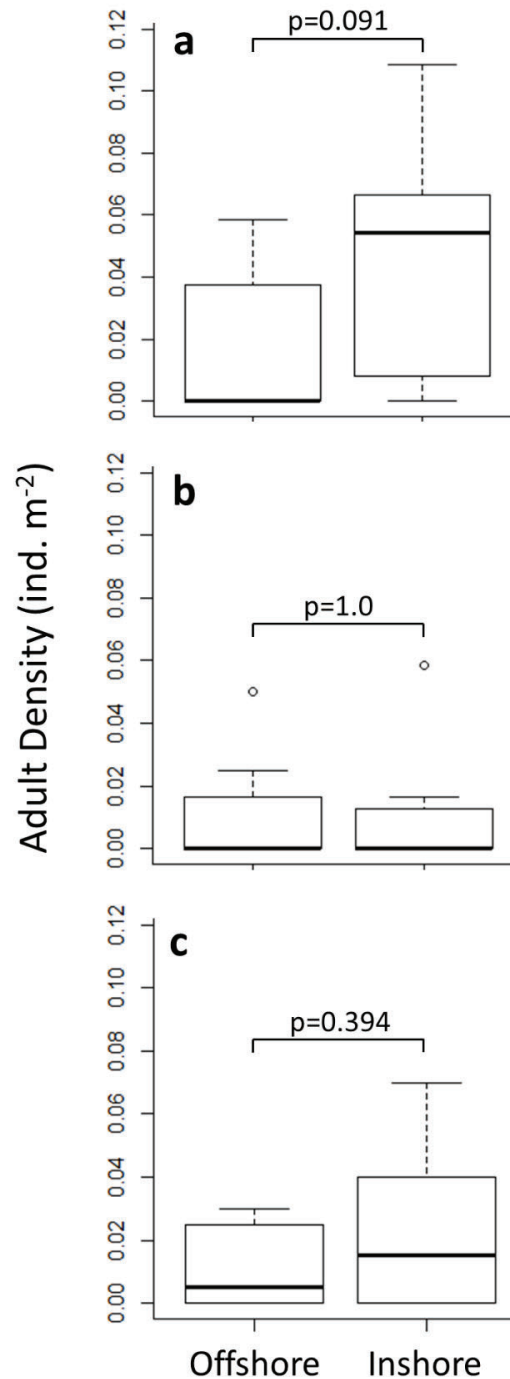


Figure 3.6. Adult *Diadema antillarum* density (ind. m⁻²) at offshore (n=8 transects) and inshore (n=12 transects) sites from (a) Pre-Irma 2017, (b) Post-Irma 2017, and (c) Post-Irma 2019 sampling dates (p-values of Mann-Whitney U tests are shown). In the box plots, horizontal box boundaries show the 25th (lower) and 75th (upper) percentiles, bold horizontal bars within the box shows median monthly settlement, whiskers show maximum (above) and minimum (below) values, and points above the boxes show outliers outside the 90th percentile.

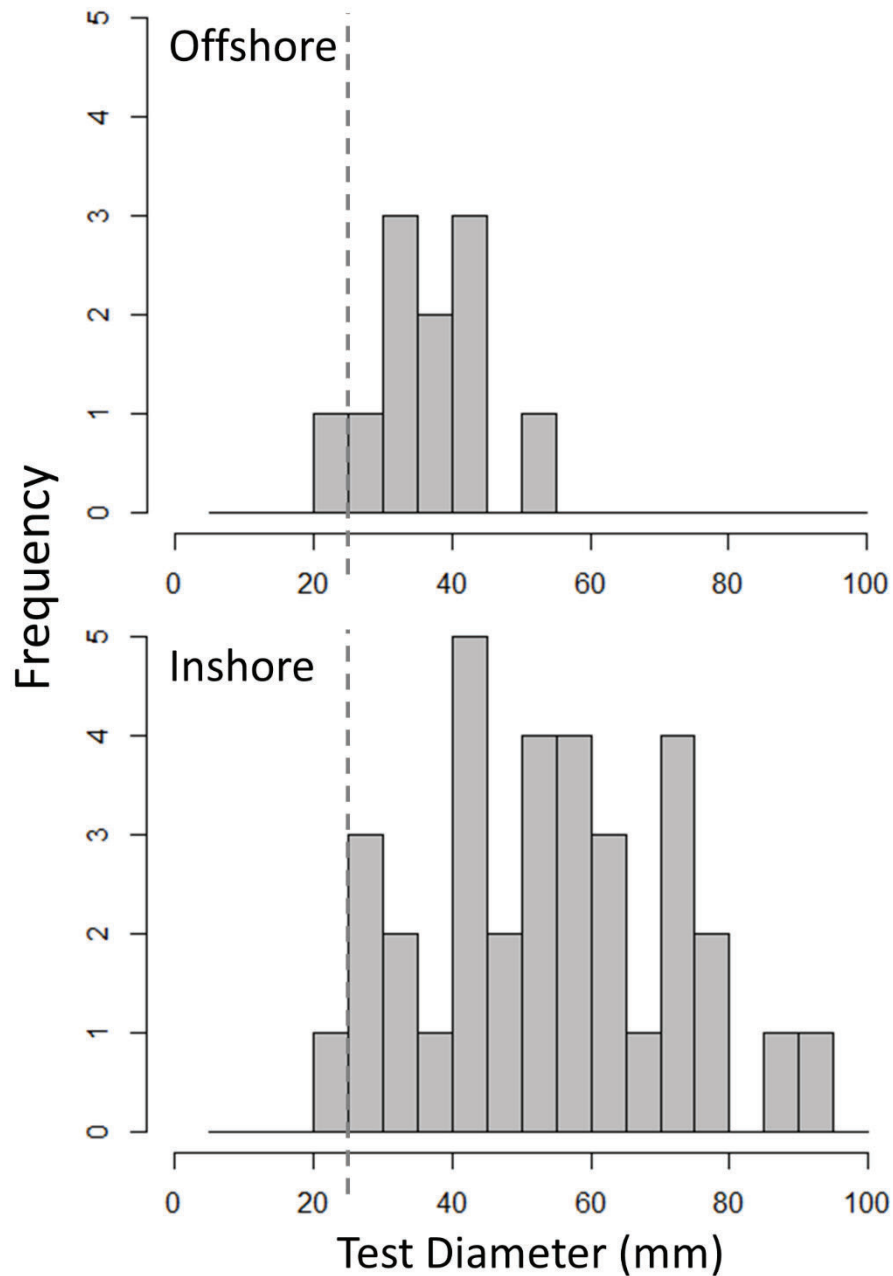


Figure 3.7. Size-frequency distributions of test diameters (mm) of benthic *Diadema antillarum* at offshore (top; n = 4 sites) and inshore (bottom; n = 6 sites) locations in the Florida Keys measured in March 2019. Test diameter size frequencies differed significantly between inshore and offshore locations (Kolmogorov-Smirnov, $p = 0.012$). Vertical dashed line represents the test diameter size (25 mm) at which *D. antillarum* are reproductively mature (Levitan 1991).

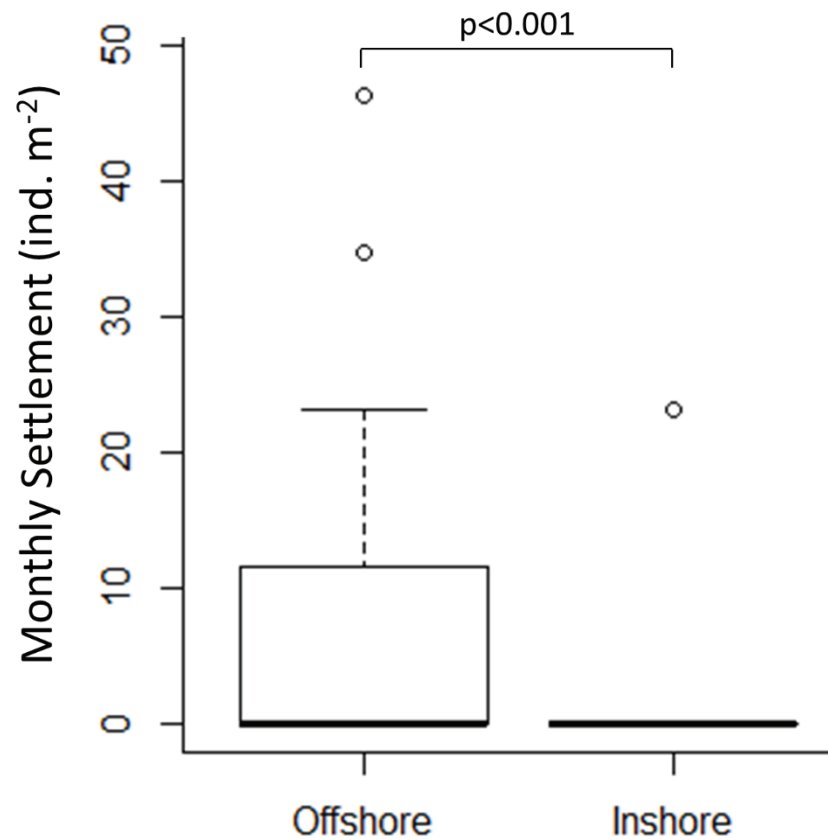


Figure 3.8. Monthly *Diadema antillarum* settlement (n = 11 months) at offshore (O1, O2, O3) and inshore (I1, I2, I3) sites in the Florida Keys (p-value for Mann-Whitney U test is shown). In the box plots, horizontal box boundaries show the 25th (lower) and 75th (upper) percentiles, bold horizontal bars within the box shows median monthly settlement, whiskers show maximum (above) and minimum (below) values, and points above the boxes show outliers outside the 90th percentile.

CHAPTER 4

DISCUSSION

The resilience of Caribbean coral reef ecosystems has been diminished by local stressors, such as nutrient loading and loss of herbivory, in addition to global shifts in ocean chemistry and climate regimes (Hughes et al. 2007). Increasing herbivory on reefs is one mechanism to strengthen ecosystem resilience and buffer against catastrophic changes to ecosystem structure following increasingly severe natural disturbances (i.e. coral bleaching, hurricanes, disease) (Hoegh-Guldberg et al. 2007). However, grazing pressure remains low on overfished Caribbean reefs since the sea urchin *Diadema antillarum* has failed to recover decades after a mass mortality event (Lessios 2016).

Florida Keys reefs have some of the lowest coral cover in the Caribbean and correspondingly low *D. antillarum* densities, indicating that the ecosystem is locally locked into an algal-dominated state stabilized by a lack of herbivory (Schutte et al. 2010; Jackson et al. 2014). Since the recovery of *D. antillarum* is predicted to locally reverse this regime shift by promoting an increase in coral recruitment (Edmunds and Carpenter 2001; Furman and Heck 2009), there is substantial motivation to understand the processes inhibiting population growth. Larval supply (Miller et al. 2009), predation (Harborne et al. 2009), habitat availability (Bodmer et al. 2015), disturbance (Forcucci 1994), and low fertilization success (Feehan et al. 2016) are some of the processes that have been suggested to limit *D. antillarum* population growth.

Here, I have identified hurricane disturbance, low larval supply, and high post-settlement mortality as factors limiting *D. antillarum* population growth in the Florida Keys. Following Hurricane Irma, *D. antillarum* densities significantly declined and benthic community composition was altered on shallow reefs in the middle and upper Florida Keys. In the subsequent months, monitoring of larval supply at several of these reefs revealed that several factors may be limiting recovery potential. Some reefs, especially inshore reefs, experience a low supply of *D. antillarum* larvae but can have moderate post-settlement survival. In contrast, *D. antillarum* larval supply to other reefs, particularly offshore reefs, is relatively higher, but post-settlement mortality may limit recruitment success. Therefore, the recovery of *D. antillarum* may depend on population growth of the upstream source of larvae to increase larval supply, and habitat enhancement in the form of coral restoration or artificial structures to promote population growth at sites with persistent larval supply.

Regime shift reversal can be difficult due to hysteresis and shifting baselines that may hinder ecosystem restoration efforts (Beisner et al. 2003, Duarte et al. 2009). In nearshore temperate ecosystems, sea urchin recruitment and changes to population dynamics can prompt a regime shift to an alternative community state (Baskett and Salomon 2010, Lauzon-Guay and Scheibling 2010). On coral reefs in the Caribbean, there is promise that the recovery of *D. antillarum* will promote similar changes, and shift the ecosystem back towards a more desirable coral-dominated state (Edmunds and Carpenter 2001, Idjadi et al. 2010). If Caribbean coral reefs are to survive the coming decades of intensifying disturbances, building ecosystem resilience by restoring herbivory must be a priority. However, it is unlikely that an essential reef herbivore, *D. antillarum*, will be able to recover without our assistance.

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